The taxonomy of *Procavia capensis* in Ethiopia, with special reference to the aberrant tusks of *P. c. capillosa* Brauer (Mammalia, Hyracoidea)

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Synopsis

Procavia capensis capillosa from the Mendebo Mountains, Bale Province, Ethiopia is redescribed, drawing attention to the peculiar shape of the upper and lower incisors which are unique amongst the Hyracoidea. The characters and distribution of all the subspecies of *P. capensis* in Ethiopia are reviewed and the classification of the genus discussed.

Introduction

Each of the two genera of rock hyraxes, *Procavia* and *Heterohyrax* (s.s.), comprises a series of apparently allopatric forms covering a large part of Africa and, in the case of *Procavia*, the Arabian Region. Both groups are notorious for the great amount of geographical variation, often of a very local nature and no doubt correlated with the high degree of isolation of suitable rocky habitats. Although many forms have been described, no satisfactory comprehensive classification exists for either group. Recent reviews are by Bothma (1971) and Roche (1972).

Several *Procavia* collected in 1972 at high altitude in the Mendebo Mountains, western Bale Province, Ethiopia by Dr D. W. Yalden, Dr P. A. Morris and Dr M. J. Largen appear referable to *P. capensis capillosa* Brauer, 1917 but show peculiarities of the upper and lower incisors that set them apart from all other known specimens of *Procavia* and indeed of Hyracoidea. These features were not, however, mentioned in the original description of *capillosa*, which was based on a single female, and appear never to have been described.

The upper tusks of normal male hyracoids are unparalleled in shape in any other mammals and are remarkably constant throughout all three extant genera. The following numbers of male specimens with permanent upper incisors have been examined without finding any deviation from the norm comparable to that seen in the specimens of capillosa: Procavia – 157, Heterohyrax s.s. – 80, Dendrohyrax – 89. The incisors of female P. c. capillosa are also distinctive but less so than those of the males.

Bothma (1971) recognized five species of *Procavia* but these have not been satisfactorily defined and I am inclined to accept the view of Roche (1972) that all should be considered conspecific. The variation thus included within one species is, however, rather extreme and much remains to be done before it is adequately described. Although the character of the tusks sets *capillosa* apart from all other hyracoids, it seems unlikely that it would give rise to reproductive isolation and I therefore propose that subspecific rank is appropriate.

Redescription of Procavia capensis capillosa

Procavia erlangeri capillosa Brauer, 1917. Type locality Adaba (=Agada), 7°00′ N, 39°24′ E, western Bale Province, Ethiopia. Holotype: Zoologisches Museum, Berlin no. 21759, skin and skull (latter originally no. 21760) of an adult female, labelled 'Agada, 8.II.01, Dr Ellenbeck'. The locality was given by Brauer as 'Agada am Abunass und Semaeno im Arussi Lande' but only one specimen was detailed. The route map in Erlanger (1904) shows 'Adaba (Agada)' at the locality shown on modern maps as Adaba. The type locality can therefore be restricted as

above. Abunass probably refers to the locality of that name much further east at about 7°25′ N, 40°25′ E but there is no evidence that *capillosa* as here understood occurs there.

Specimens examined. The holotype skull; also the following, all from the Mendebo (Bale) Mountains, near Dinshu (=Gurie), 7°06′ N, 39°47′ E and up to 20 km westwards ('Shifta Rock' between Dinshu and Adaba), at altitudes from 3100 to 3500 m. All but the first two were found as skulls and therefore were not sexed other than by the tusks.

BMNH 1972.1078 3 ad.	skull, skin	M ³ erupted, moderately worn
BMNH 1972.1079 ♂ ad.	skull, skin	M³ erupted, moderately worn
BMNH 1972.1080 ? ad.	skull only	M³ erupted, no mandibles, no incisors
BMNH 1972.1081 ? ad.	skull only	M ₃ erupted, mandibles only
BMNH 1972.1082 [♀] subad.	skull only	M ² erupted, complete
BMNH 1972.1083 ? ad.	skull only	M ³ erupted, no incisors
BMNH 1972.1084 ? juv.	skull only	P ¹⁻⁴ only, no upper incisors
BMNH 1972.1077 [♀] ad.	skull only	M ³ erupting, no mandibles
BMNH 1976.121 [♀] ad.	skull only	M ³ erupting, no mandibles
BMNH 1976.122 ? juv.	skull only	P ¹⁻³ only

DIAGNOSIS. Pelage long and dense; dorsal flash black; upper incisors of males and females convergent, with flat anterior surfaces; lower incisors parallel; P_1 generally absent in adults; P_1 generally present and double-rooted.

DESCRIPTION. Pelage long, dense and soft, containing many fine, wavy wool fibres (seen elsewhere in the genus only in *P. capensis mackinderi* from comparable altitudes on Mount Kenya). Dorsal pelage creamy brown with dark grey hair-bases showing, giving an irregular mottled appearance (as in *P.c. erlangeri* but much less orange) rather than a neat agouti effect. Grey bases concealed more effectively on nape, giving pale collar. Head darker than back, especially on cheeks and around eyes, but much less dark than in *P. c. erlangeri*. Hairs around dorsal gland black, much more prominent than in *P. c. erlangeri* but rather less prominent than in *P. c. scioana*. Slight yellow spot on hind margin of black patch. Naked glandular area about 15–20 mm wide and 30–35 mm long. Ventral pelage creamy buff, much less orange than in *P. c. erlangeri*, similar to *P. c. scioana* and many other forms. Feet similar in colour to back. Vibrissae black, distributed as in other *Procavia*.

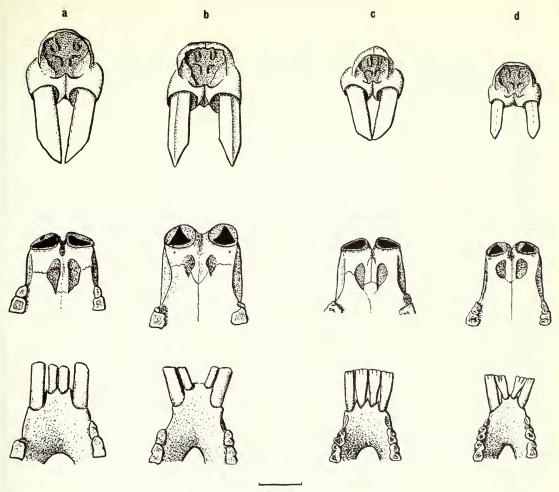
Skull differing from that of other *Procavia* in the following features (Fig. 1): upper incisors of adult males convergent, with flat anterior surfaces; of adult female similar but smaller and less angular, although much flatter and wider than in females of other subspecies; lower incisors parallel in both sexes. The two adult male skulls also lack any ridge or overhanging crest on the maxilla below the anteroventral margin of the orbit (a condition normal in females elsewhere but rare in adult males). A three-pronged pectination of the lower incisors is visible on all four teeth of the presumed female with M² erupted (1972.1082) but not on the much more worn teeth of the fully adult males.

 P^1 is lacking on both sides in one of the adult males (slightly the older judging by tooth-wear and cranial crests) but present and double-rooted in the other and in the four other fully adult skulls. In the subadult female it is present only on the left. P_1 is lacking in all six adult or subadult mandibles, although single alveoli are present in one (M_3 erupted).

In the holotype, a presumed female, the upper incisors are less convergent than in the others, leaving a gap of 2 mm between the tips, but they are nevertheless quite different in shape from those of either sex of other races.

MEASUREMENTS (Table 1). Similar in size to other large forms of P. capensis, e.g. P. c. scioana and P. c. erlangeri.

Measurements of the only adult animal measured in the flesh (BMNH 1972.1079, ♂, M³ moderately worn): head and body 555 mm; hind feet 75 mm; ear 35 mm; weight 4.25 kg.



10 mm

Fig. 1 Incisors of *Procavia capensis* from Ethiopia.

Top: anterior view of upper incisors; centre: ventral view showing, in black, the upper incisors as they would appear in transverse section at the alveoli; bottom: dorsal view of lower incisors.

(a) *P. c. capillosa*, Bale Prov., adult β (M³ worn), BMNH 1972.1079; (b) *P. c. erlangeri*, Dire Dawa, Harar Prov., adult β (M³ worn), BMNH 34.11.20.8; (c) *P. c. capillosa*, Bale Prov., subadult φ (M² erupted), BMNH 1972.1082; (d) *P. c. erlangeri*, Dire Dawa, Harar Prov., subadult φ (M² erupted), BMNH 34.11.20.6.

HABITAT. Rocky outcrops between 3100 and 3500 m in *Erica arborea* and *Juniperus* zones much degraded by heavy grazing to a mosaic of grass and scrub (D. Yalden, in litt.).

Variation of *Procavia* in Ethiopia

The localities shown on the map (Fig. 2) represent the specimens of *Procavia* from Ethiopia in the collection of the British Museum (Natural History) that are sufficiently localized, along with the few others that have been seen or that have been reported in the literature in sufficient detail. A general distinction can be made between the high altitude forms, which are variable but large, dark and with a black or obscure dorsal flash, and the forms in the surrounding lowland savanna and steppe zones. These latter appear much more uniform than is suggested by the existing litera-

Table 1 Characteristics of the principal forms of Procavia capensis in Ethiopia.

	habessinica	scioana	capillosa	erlangeri	jacksoni
No. of ad. skins examined	14	25	2	10	2
Dorsal flash	Yellow and black, obscure	Black, large	Black, Black, moderately large obscure	Black, obscure	Yellow, large
Dorsal pelage	Dark, greyish Dark, fai brown, rather uniform speckled	Dark, faintly n speckled	Greyish brown, mottled	Orange brown, mottled	Brown, speckled (agouti)
Head	Slightly darker than back	Slightly darker than back	Darker than back	Dark, almost black	Slightly darker than back
Woolly underfur	0	0	+	0	0
Feet (upper surface, cf. back)	Same	Paler	Same	Darker	Same
Size (ads with M³) Head and body (mm) Condylobasal length (mm) P¹-M³ (mm)	c. 450 80-91 (10) 35-40 (12)	c. 500 89–102 (6) 37–42 (9)	555 (1) 94-99 (5) 39-45 (6)	465, 510 (2) 87–97 (4) 39–42 (5)	535 (1) (87–M² only)

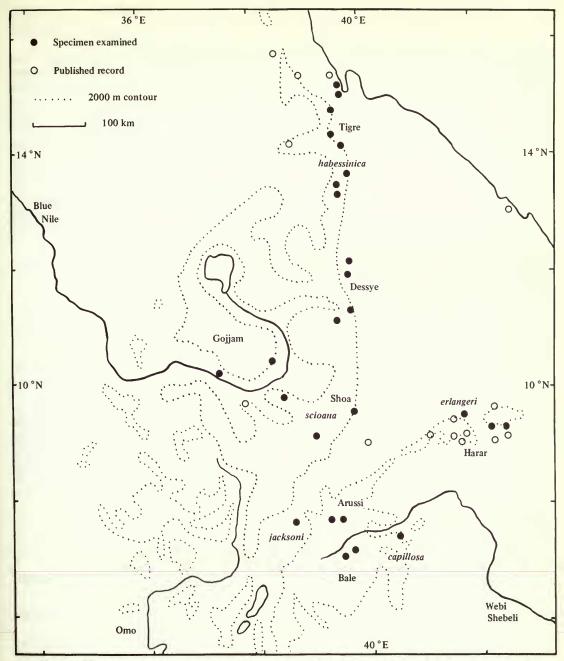


Fig. 2 The Ethiopian Highlands showing localities from which Procavia has been recorded.

ture. A 'typical savanna' form can be recognized ranging from northern Tanzania (matschiei Neumann, 1900) through Kenya and Uganda, and across the savanna zone to Senegal, characterized especially by agouti pelage and large yellow dorsal flash. Unfortunately the older names that might apply to this form all relate to divergent peripheral populations – pallida Thomas, 1891 (Somalia), latastei Thomas, 1892 (Senegal), kerstingi Matschie, 1899 (Dahomey). This form penetrates Ethiopia from the south along the Rift Valley (specimens in BM(NH) from Lake Langano) where it can provisionally be called P. c. jacksoni Thomas, 1900; it probably also occurs

in the southeast (Ogaden) in the form of the very small *P. c. pallida* Thomas, 1891; and probably extends from the west up the Blue Nile where it may be represented by *P. c. meneliki* Neumann, 1902.

In the north, the steppe/desert form resembles the savanna form except that the pelage is more uniformly yellow-brown without marked agouti speckling, the head is not noticeably darker than the back and the dorsal flash, although yellow, is less conspicuous and contrasting. This form extends from Sudan north to Sinai and Lebanon and can be called *P. c. syriaca* with ruficeps as a synonym – there is no case for using the name ruficeps (type-locality Dongola in northern Sudan) for the more southern savanna form as is so often done, e.g. by Bothma (1971) and Roche (1972). This form probably occurs in northern Ethiopia and may intergrade with the northern highland form habessinica. In the south, on the other hand, it seems likely that the high altitude forms are more isolated from the savanna forms by forest, although any such isolation may well be breaking down with the destruction of forest.

The characters of the four highland subspecies that can be recognized are summarized in Table 1, along with those of *P. c. jacksoni* representing the savanna form. These subspecies are briefly reviewed below together with intermediate populations from possibly isolated segments of the plateau.

Highland forms

P. c. habessinica (Hemprich & Ehrenberg, 1828)

TYPE LOCALITY. Arkiko, near Massawa, N.E. Ethiopia.

SYNONYMS. Euhyrax abyssinicus Gray, 1868; Hyrax alpini Gray, 1868; Hyrax ferruginea Gray, 1869; Hyrax irroratus var. luteogaster Gray, 1869 (all from 'Abyssinia'); Procavia abyssinica minor Thomas, 1892, Alali, Red Sea Coast, 13° N.

REMARKS. This form can be recognized along the mountain chain between Massawa on the coast and the region of Quiho and Antalo (13°20′ N) at altitudes up to 2500 m. The presence in the dorsal flash of some hairs with extensive yellow tips makes it somewhat intermediate between *scioana* of the central highlands and *syriaca* in eastern Sudan, but the overall dark colour and dark head are in clear contrast with the uniform yellowish brown of *syriaca* (=burtoni). To the south, specimens from the Dessye region are intermediate in size and in the prominence of the black dorsal flash between habessinica and the larger P. c. scioana.

P. c. scioana (Giglioli, 1888)

TYPE LOCALITY. Ankober, Shoa, central Ethiopia.

SYNONYMS. Procavia shoana Thomas, 1892; ? Procavia butleri Wroughton, 1911, Jebel Fazogli, Blue Nile, Ethiopia/Sudan border.

REMARKS. Found in the mountains of Shoa, around 3000 m, possibly forming a cline with the smaller P. c. habessinica to the north.

The few specimens seen from Gojjam, i.e. northwest of the Blue Nile Gorge, are similar but smaller (condylobasal length of five adults 83–89 mm) and one of the eight skins has the dorsal flash brown rather than black. The form *butleri* has the dorsal flash black but indistinct and can be considered a peripheral highland form.

Specimens from the Arussi Mountains, i.e. southeast of the Rift Valley but north of the Webi Shebeli, appear in some respects intermediate between P. c. scioana and P. c. capillosa. They are large (condylobasal length of the three adults measured 103, 105 and 109 mm, P¹-M³ 44, 45, 45 mm) and have the dorsal flash black but less prominent. One adult male (Field Museum 27090) has the upper incisors like those of capillosa in section although rather thicker, and parallel as in normal Procavia. Another adult male from the same locality, Tichu (c. 7°45' N, 39°30' E), has the tusks normal in every respect.

P. c. capillosa Brauer, 1917

Type Locality. Adaba, Mendebo Mts.

REMARKS. This form may be isolated from that in the Arussi Mts to the north by the Webi Shebeli and is probably confined to the mountains of Bale Province.

P. c. erlangeri Neumann, 1901

Type Locality. Upper Webi Shebeli, especially around Harar, Ethiopia.

SYNONYM. Procavia erlangeri comata Brauer, 1917, Gara Mulata Mts, west of Harar.

REMARKS. The original description agrees well with specimens in the British Museum (Natural History) from around Harar. The black head, yellowish colour and virtual absence of a dorsal flash make this a very distinctive form. The form *comata* was distinguished only by the greater length of the pelage, and can be considered consubspecific. Ingersol (1968) commented on the uniformity of specimens from a wide range of habitats in the Harar area.

Lowland forms

P. c. pallida Thomas, 1891

Type Locality. Hekebo Plateau, N. Somalia.

REMARKS. A small form – condylobasal length of an adult female with M³ worn 73.8 mm, P¹-M³ 31.0 mm. The agouti pelage and yellow dorsal flash relate it to the savanna form.

P. c. jacksoni Thomas, 1900

Type Locality. Ravine Station, Kenya.

REMARKS. The sole fully adult specimen from the southern Rift Valley of Ethiopia (Lake Langano) has the dorsal flash prominent and yellow. The crown is slightly rufous, contrasting with the paler yellowish brown back with agouti speckling. This specimen was incorrectly called *P. habessinica alpini* by Corbet & Yalden (1972). Specimens of *jacksoni* in Kenya are rather darker and have the dorsal flash less prominent although comprising wholly yellow hairs.

P. c. syriaca (Hemprich & Ehrenberg, 1828)

Type Locality, Mount Sinai.

SYNONYMS. Hyrax ruficeps Hemprich & Ehrenberg, 1832, Dongola, N. Sudan; Hyrax burtoni Gray, 1868, Egypt.

REMARKS. This form occurs from the northern extremity of the range of the genus, in Lebanon, through Egypt and the Sudan, merging with the savanna form in southern Sudan (specimens from around Khartoum are intermediate), and possibly with *P. c. habessinica* in the hills of extreme northern Ethiopia and eastern Sudan. Setzer (1956) postulated that two species were sympatric in northeastern Sudan, calling them *P. habessinica burtoni* and *P. ruficeps ruficeps* but this appears to have been based on the variable allocation of old specimens from Dongola on the Nile – there has never been a clear demonstration of sympatry of any two forms of *Procavia* at one locality.

Variation of *Procavia* throughout its range

A more superficial examination of specimens from the entire range of the genus suggests the following major groups, some of them with considerably modified local or peripheral variants. capensis – southern Africa; dorsal flash black; dorsal pelage finely speckled, head usually

no darker than back; P₁ usually absent but present at the northeastern extremity (johnstoni, Malawi).

welwitschi - Angola/Namibia; dorsal flash yellow, P₁ usually absent.

syriaca – savanna zone from northern Tanzania to Somalia and Senegal, and north through Sudan to Egypt, Sinai, Lebanon and Arabia; dorsal flash yellow, usually clearly defined; dorsal pelage agouti in savanna zone with head darker; more uniform yellowish brown north of Khartoum with head no darker than back; P₁ usually present. Moderately differentiated forms occur on the periphery: Mt Nimba, Mauritania, Hoggar, Jebel Marra, Mt Kenya, Somalia, Arabia.

habessinica – Ethiopian plateau; dorsal flash black or obscure; not strongly agouti, head often dark; P₁ variable; many local variations, some very close to capensis s.s.

It is tempting to recognize these as discrete species but they are very difficult to diagnose. In the north the *syriaca* group appears to intergrade with the *habessinica* group in northern and perhaps western Ethiopia. There is a wide gap, from northern Tanzania to southern Malawi, apparently without *Procavia*. The widespread *capensis* s.s in southern Africa is scarcely distinguishable from some members of the *habessinica* group, especially *scioana* from which it differs only in the usual absence of P₁. The southwestern *welwitschi* seems discretely separable from the adjacent *capensis* but is only separable from some of the *syriaca* group by the absence of P₁ which is not constant (Roche, 1972).

The principal difference between this and previous classifications is the separation of *matschiei* (northern Tanzania) and other east African forms with the dorsal flash yellow from *johnstoni* (southern Malawi, dorsal flash black) which is here seen as a peripheral relative of the southern *capensis* s.s. In spite of the great difference in external appearance and wide geographical separation these were considered conspecific (in a split classification) by Hahn (1934), followed by many other authors, mainly on the basis of well-developed P₁.

Heterohyrax in Ethiopia

Heterohyrax brucei occurs throughout most of Ethiopia, sometimes occupying the same rock outcrops as Procavia, and their separation in the field can be difficult. The most useful characteristics for recognizing Heterohyrax are: dorsal pelage short, neat, agouti; dorsal flash small, discrete, pale cream to rust-orange, hairs concolorous to roots; head scarcely darker than back; discrete pale streak above eye (Procavia sometimes has a more diffuse pale zone surrounding the eye or above and behind the eye); ventral pelage grey, less yellowish than in Procavia. Size is never so great as in the large forms of Procavia (rarely over 480 mm head and body) but colonies of one species show a great range of sizes at any one time due to slow attainment of full adult size. In the hand the clearest external distinction in adult males is the anterior position of the penis in Heterohyrax – about 60–70 mm in front of the anus compared with 20–30 mm in Procavia.

Immature skulls can be difficult to distinguish but adult skulls of *Heterohyrax* have the teeth rather uniform in size, with the combined length of M^1-M^3 shorter than P^1-P^4 whereas in *Procavia* M^1-M^3 are conspicuously large and together considerably larger than P^1-P^4 .

Summary

- 1. Procavia capensis capillosa from the Mendebo Mts, Bale Province, Ethiopia is distinguishable from P. c. scioana to the north and P. c. erlangeri to the northeast by its woolly pelage and from these and all other hyracoids by the formation of the incisors uppers convergent, with flat anterior surfaces in both sexes, lowers parallel (consistent, allowing for sexual dimorphism, amongst all seven specimens).
- 2. The forms *erlangeri*, *capillosa*, *scioana* and *habessinica* form a distinctive, although variable, group in the Ethiopian Highlands with the last showing characters approaching the adjacent lowland *P. c. syriaca*.
- 3. Four main regional groups are recognized in *P. capensis*, distinguished by overall colour of the dorsal pelage and especially of the 'dorsal flash' around the mid-dorsal gland: *capensis* s.s. and *welwitschi* in southern Africa, *syriaca* in the northern savanna and arid zones and *habessinica* in the Ethiopian highlands.

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References

References to original descriptions can be found in Allen (1939).

Allen, G. M. 1939. A checklist of African mammals. Bull. Mus. comp. Zool. 83: 1-763.

Bothma, J. du P. 1971. Part 12, order Hyracoidea, 8 pp. In Meester, J. & Setzer, H. W. (eds) The mammals of Africa: an identification manual. Washington.

Brauer, A. 1917. Neue Procaviiden. Sber. Ges. naturf. Freunde Berl.: 294-303.

Corbet, G. B. & Yalden, D. W. 1972. Recent records of mammals (other than bats) from Ethiopia. Bull. Br. Mus. nat. Hist. (Zool.) 22: 211-252.

Erlanger, C. F. von 1904. Beitrage zur Vogelfauna Nordostafrikas. J. Orn. 52: 137-244, maps 1-3.

Hahn, H. 1934. Die Familie der Procaviidae. Z. Säugetierk. 9: 207–358.

Ingersol, R. H. 1968. The ecological significance of mammals in the eastern Chercher Highlands of Harar Province, Ethiopia. Ph.D. thesis, Oklahoma State University.

Roche, J. 1972. Systematique du genre Procavia et des damans en general. Mammalia 36 : 22-49.

Setzer, H. W. 1956. Mammals of the Anglo-Egyptian Sudan. Proc. U.S. nat. Mus. 106: 447-587.